

Breeding ecology of Horned Puffins (*Fratercula corniculata*) in Alaska: annual variation and effects of El Niño

A.M.A. Harding, J.F. Piatt, and K.C. Hamer

Abstract: Both within and among seabird species, different aspects of breeding biology may respond to changes in prey availability in distinct ways, and the identification of species-specific breeding parameters that are sensitive to food availability is useful for monitoring purposes. We present data from a 5-year study (1995–1999) of the breeding ecology of Horned Puffins (*Fratercula corniculata*) in Alaska. The El Niño – Southern Oscillation event of 1997–1998 provided an opportunity to examine the sensitivity of various breeding parameters to a reduction in prey availability caused by the anomalous oceanographic conditions of 1998. Horned Puffins were able to maintain high fledging success (83–97%) over the 5 years of the study, despite the poor local feeding conditions in 1998. The rate of increase in chick mass was lowest in 1998, and evidence suggests that chicks also fledged at the youngest ages in that year. The impacts of reduced food availability on growth varied among body structures, suggesting differential allocation of energy and nutrients. There was no variation among years in either chick diet or the mass of food loads delivered by adults. We suggest that rates of chick growth, specifically mass increase, may be a good parameter to measure for use in monitoring Horned Puffins.

Résumé : Les différentes composantes de la biologie de la reproduction d'une espèce d'oiseau marin peuvent réagir de façon particulière aux changements de disponibilité des proies et varier d'une espèce à l'autre; de plus, l'identification des paramètres de la reproduction sensibles à la disponibilité de la nourriture et propres à chaque espèce est utile pour la surveillance écologique. On trouvera ici des données provenant d'une étude de 5 ans (1995–1999) de l'écologie de la reproduction chez le macareux cornu (*Fratercula corniculata*) en Alaska. Le phénomène d'El Niño – oscillation australe de 1997–1998 a fourni l'occasion de vérifier la sensibilité des divers paramètres de la reproduction à la réduction de la disponibilité des proies due aux conditions océaniques anormales de 1998. Les macareux cornus ont réussi à mener un fort pourcentage de leurs petits jusqu'à l'envol (83–97 %) durant les 5 années de l'étude, malgré les mauvaises conditions alimentaires locales en 1998. Le taux de croissance en masse des poussins a été plus faible en 1998 et il y a des indices que les petits ont pris leur envol à des âges plus jeunes cette année-là. Les effets de la disponibilité réduite de nourriture sur la croissance a varié d'une structure à l'autre du corps, ce qui laisse croire à une allocation différentielle de l'énergie et des nutriments à la croissance des différentes structures. Il n'y avait pas de différences d'une année à l'autre entre les régimes alimentaires des poussins, ni entre les charges de nourriture apportées par les parents. Nous croyons que les taux de croissance des poussins, en particulier le taux de croissance en masse, peuvent être des paramètres utiles à mesurer pour la surveillance écologique des macareux cornus.

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Introduction

The life histories of seabirds are characterized by long life-spans, deferred maturity, and low annual reproductive output (Charlesworth 1980; Ricklefs 1990). These traits are generally thought to reflect a low ceiling on annual reproductive output because of the sparse, patchy, and unpredictable distribution of marine food resources (Lack 1968). According to life-history theory, breeding adults trade off fu-

ture reproduction against current investment (Stearns 1992), and in variable environments they should adjust their behaviour during each breeding attempt to maximize their lifetime reproductive success (Williams 1966). Where food availability is low, adults should abandon a breeding attempt if risks to survival are too high (Drent and Daan 1980), because a small reduction in adult survival in long-lived species has a large negative impact on lifetime reproductive output (Charlesworth 1980).

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Many studies have demonstrated that food availability can have a profound effect on breeding in seabirds (e.g., Monaghan et al. 1989; Hatch and Hatch 1990; Hamer et al. 1991; Danchin 1992), and species may exhibit high variability, both geographically and at the same colony, within certain breeding parameters among years. For example, there is well-documented evidence that Atlantic Puffins (*Fratercula arctica*) respond to poor food availability with reduced growth rates, extended fledging periods, shifts in chick diet, and even complete breeding failure (e.g., Barrett and Rikardsen 1992).

Both within and among seabird species, there may be considerable variability in how individuals respond behaviourally and biologically to fluctuations in prey availability (Cairns 1987; Baird 1990). For example, small species such as the Common Tern (*Sterna hirundo*) may spend a high proportion of their time feeding and have little flexibility in dealing with food shortages compared with large species such as the Common Murre (*Uria aalge*) that may be able to adjust time budgets and buffer breeding success against food shortages (Pearson 1968; Monaghan et al. 1989, 1994). How animals deal with fluctuations in food abundance can be examined in light of their life histories, physiological and ecological constraints, and how they allocate resources to reproduction, growth, and survival. There is still a need for data on differential responses to food availability among species with contrasting life histories (Monaghan 1996; Ricklefs 2000).

The identification of breeding parameters that are sensitive to food availability is also crucial for monitoring. There has been much interest in seabirds as monitors of changes in marine ecosystems (Cairns 1987; Harris and Wanless 1990; Montevecchi 1993), and many studies have identified species-specific breeding parameters as key indicators of local oceanic conditions (e.g., Burger and Piatt 1990; Monaghan et al. 1994).

This paper presents data on the breeding ecology of the Horned Puffin (*Fratercula corniculata*), one of three North Pacific puffin species with a summer distribution ranging in latitude from 50° to 72°N (Amaral 1977). Although the Atlantic Puffin has been studied extensively (e.g., Ashcroft 1979; Harris 1984, 1985), relatively little information exists on the breeding ecology of the larger congeneric Horned Puffin. In contrast to the other species of puffin, the Horned Puffin almost always nests among boulders or in rock crevices, making access to nest sites and chicks difficult and complicating the study of their breeding biology. Consequently, sample sizes are small for many breeding parameters and little is known about annual or geographic variation in breeding ecology (Piatt and Kitaysky 2002). We present data from a 5-year study (1995–1999) on the breeding ecology of Horned Puffins in Lower Cook Inlet, Alaska. The main purpose of this study was to increase our knowledge of the annual variability in different breeding parameters at a single colony. In addition, the El Niño – Southern Oscillation (ENSO) event of 1997–1998 presented an opportunity to examine how various breeding parameters responded to the anomalous oceanographic conditions and relatively poor food supplies of 1998. We examine the response and relative sensitivity of different breeding parameters to variation in food availability and make recommendations for monitoring puffins.

Materials and methods

Study site

This study was conducted on Duck Island, a small island located about 0.4 km off the east of Chisik Island in western Cook Inlet, Alaska, U.S.A. (60°09'N, 152°34'W). An estimated 2000 pairs of Horned Puffins nest in caves and in crevices amongst the boulders on Duck Island (Harding 2001).

Productivity and time of breeding

Puffins are sensitive to disturbance during the incubation phase of their breeding cycle, and may respond by abandoning breeding (Lockley 1934; Harris 1984; Rodway et al. 1996). So nests were not disturbed until late in the incubation period, when the island was searched for active nest sites with visible nest chambers. Active nest sites were marked and visited every 3–5 days until hatching. During each visit the nest chambers were checked using a headlamp, and the presence of adult, egg, or chick was recorded. Where an adult blocked the sight of an egg or chick, the adult's brooding posture and the presence of eggshell fragments were used as evidence of hatching. In the few nest chambers where chicks could move out of sight, chick vocalization and the presence of dropped meals in the nest chamber provided additional evidence of hatching. Median chick hatch date was used as a measure of annual timing of breeding.

Fledging success was calculated each year. Hatching success and breeding success were also calculated. Both these parameters were likely to be overestimated because nest sites were not located until late in incubation, before which some eggs may have been laid and lost. Nonetheless, they provide a useful index of reproductive success that can be compared among years. The timing of the first nest check during incubation varied among years (23 June to 16 July). To control for a possible bias in recorded egg loss and therefore maximum hatching success in different years, all nest sites where an egg was followed and lost before July 15 were excluded from calculations of annual hatching and breeding success.

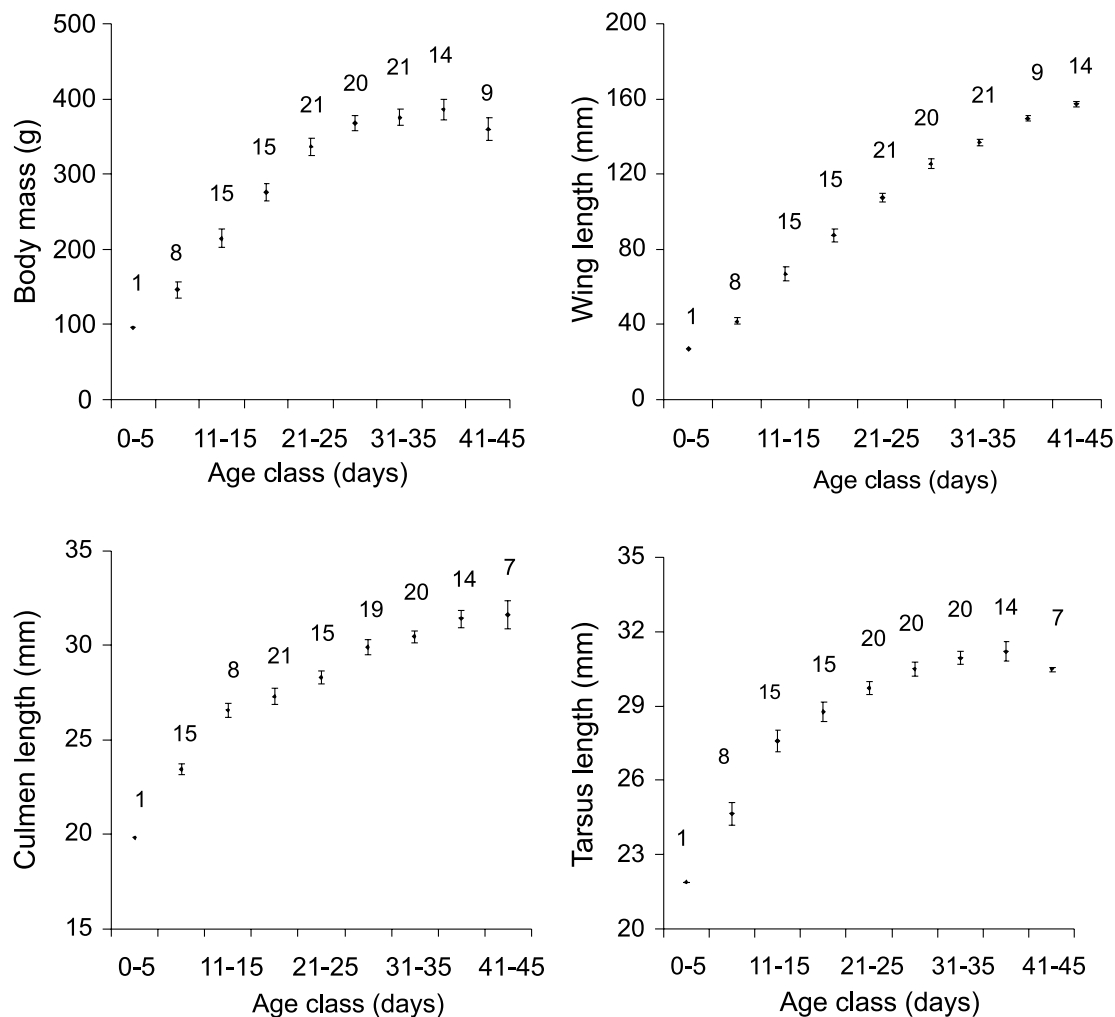
Owing to deteriorating weather conditions and the departure of field crews at the end of each field season, only 47% of chicks were followed to fledging during the 5 years. Of a total of 161 chicks from all 5 years, 20 (12%) were known to have died in the nest, with 80% of these deaths occurring at 10 days of age or less, and no mortality after 20 days of age. To calculate fledging success, chicks ≥ 20 days old at the end of fieldwork were thus considered to have survived until fledging.

Dead chicks were not removed from the nest by parents or predators. Although there can be no certainty of successful fledging, we assumed that fully feathered chicks (aged >25 days) that disappeared from the nest between visits had fledged. Owing to the early departure of field crews in some years, fledging age was calculated only in 1996, 1998, and 1999.

Chick measurements

Chicks were visited every 4–7 days during the chick-rearing period and every 3–5 days during the fledging pe-

Fig. 1. Growth (mean \pm 1 SE) of Horned Puffin (*Fratercula corniculata*) chicks in 1999. The number above each age class is the sample size ($n = 28$ chicks in total).



riod. During each visit, the following body dimensions were measured (following Wernham and Bryant 1998): tarsus length (± 0.1 mm), using vernier calipers; culmen length, using vernier calipers, from the tip of the maxilla to the anterior edge of the growing cere; straightened wing length (± 0.1 mm), using a stopped ruler; and body mass (± 1.0 g), using a Pesola balance. Repeat measurements, taken in accordance with the procedure recommended by Barrett et al. (1989), were within 0.2 mm for tarsus and culmen lengths, 1.0 mm for wing length, and 1.0 g for body mass. Chicks were first handled when they were older than 5 days and the parents had finished brooding. For the few nest sites with accessible chicks that were found later in the season, for which the hatch date was unknown, chicks were aged using a linear regression of age on wing length for chicks of known age ($n = 67$). A proportion of known-age chicks ($n = 40$) were aged to within 88.8% of their absolute age using the predicted value.

To compare growth among years, the growth rate of different body components during the linear phase of growth (10–30 days for body mass and wing length and 0–15 days for culmen and tarsus lengths; Fig. 1) was calculated using linear regression. These data were used to calculate a single

growth rate for each body component of each chick, averages of which were then compared among years using analysis of variance (ANOVA) followed by post-hoc range tests.

Chick diet

The diets of Horned Puffin chicks were assessed throughout the chick-rearing period each year (at different nest sites from those used to estimate productivity and chick growth) using the following four methods: (1) Entrances to ca. 15 nest sites were temporarily blocked using wire-mesh screens (Hatch and Sanger 1992). After ca. 2 h, nest sites were revisited, screens were removed, and food samples dropped by adults at the nest entrance were collected. (2) Gill nets (2–3 cm mesh) or mist nets were draped over boulder piles, blocking the entrances to several puffin nest sites simultaneously, and observed from a distance. Adults caught in the nets were immediately removed and measured prior to release; any dropped food items were collected. (3) Food loads were sometimes dropped by flying or landing adult puffins, particularly when they were startled by a worker's presence. Freshly dropped fish were collected opportunistically throughout each season. Many complete bill loads were collected

Table 1. Horned Puffin (*Fratercula corniculata*) productivity and timing of breeding in different years.

Year	1995	1996	1997	1998	1999	χ^2	df	P
Total number of nests	21	51	48	61	47			
Hatching success	0.71	0.84	0.67	0.69	0.77	5.19	4	>0.5
Fledging success	0.92	0.83	0.96	0.89	0.97	4.71	4	>0.5
Breeding success	0.66	0.70	0.64	0.62	0.70	5.19	4	>0.5
Median chick hatch date	21 July	19 July	25 July	29 July	26 July			

Note: Hatching, fledging, and breeding success are compared between years using χ^2 contingency tables. All tests are nonsignificant, with 4 degrees of freedom.

Table 2. Measurements of Horned Puffin fledglings in 1999.

	Mean	n	SD
Age (days)	40.7	28	4.1
Mass (g)	400.6	16	45.2
Wing length (mm)	155.8	16	5.2
Tarsus length (mm)	31.3	16	1.3
Headbill length (mm)	70.2	15	1.7
Culmen length (mm)	31.9	16	1.6

whilst working in large caves with several Horned Puffin nests. (4) Puffins sometimes stand outside their nest site for a short time before provisioning their chick. Bill loads held by adult puffins standing on boulders and cliffs in the colony were recorded. Prey species were identified using 10 × 42 binoculars and the fish in the bill were counted.

All prey collected were identified (using taxonomic keys; Hart 1973), weighed (using an electronic balance, ± 0.01 g), and measured (length to tail fork, using a steel ruler with a precision of ± 0.1 mm). All prey items were weighed and measured within 2 h of collection. Energy content of prey was calculated using published wet-mass energy-density conversions (Van Pelt et al. 1997). All meal collections were identified as either a complete or an incomplete bill load. Items classified as complete bill loads were either observed dropped loads, observed gill-net loads where no fish were lost, or visual identifications.

Adult measurements

Breeding adult Horned Puffins were measured in 1998 and 1999 to examine the proportion of adult body size reached by fledglings. Adults were captured at their nest during the chick-rearing period by hand or by using a gill net placed over the nest entrance during food delivery. The same body measurements were taken as for chicks.

Results

Productivity and timing of breeding

Hatching success varied among years from 67 to 84% of eggs, and fledging success varied from 83 to 97% of chicks. No eggs were depredated and eggs that failed to hatch were cracked or addled as a consequence of either embryo death or a lack of fertilization. There was no variation among years in hatching success, fledging success, or breeding success ($P > 0.05$ in all cases; Table 1). Median chick hatching dates ranged from 19 July in 1996 to 29 July in 1998. There was significant variation in median chick hatching date

among years (Kruskal–Wallis ANOVA, $H_{[4]} = 39.05$, $P < 0.001$; Table 1), with the median hatch date earlier in 1996 than in 1997, 1998, and 1999 and earlier in 1995 than in either 1998 or 1999 (non-parametric multiple comparisons (Zar 1996), $P < 0.05$).

Chick growth and fledging

Fledging success was highest (97%) in 1999, so we took this year to indicate chick growth during favourable conditions. Figure 1 shows the growth of body mass and external measurements in 1999. There was an initial rapid linear increase in mass (10.8 g/day, on average) until about 30 days of age. This linear phase of growth was followed by a period of very slow mass gain (1.39 g/day, on average), up to a peak of 386 ± 51.9 g (mean \pm SD) at about 38 days. A short period of mass recession (1.25 g/day, on average) then occurred prior to fledging. Adult body mass was 531 ± 44.0 g (mean \pm SD; $n = 21$), and chicks in 1999 fledged, on average, at 75.5% of this mass (Table 2).

Wing, culmen, and tarsus lengths had different growth trajectories (Fig. 1). Wing length increased more or less linearly throughout the nesting period, and the wing length of chicks at the last check before fledging was 156 ± 5.2 mm (mean \pm SD; $n = 16$), which was 79.2% of adult wing length (197 ± 5.5 mm (mean \pm SD); $n = 21$). In contrast, the tarsus had a longer decelerating period of growth, and tarsus lengths of fledglings were very similar (within 2%) to those of adults (adult tarsus length = 31.9 ± 2.1 (mean \pm SD); $n = 21$; Table 2).

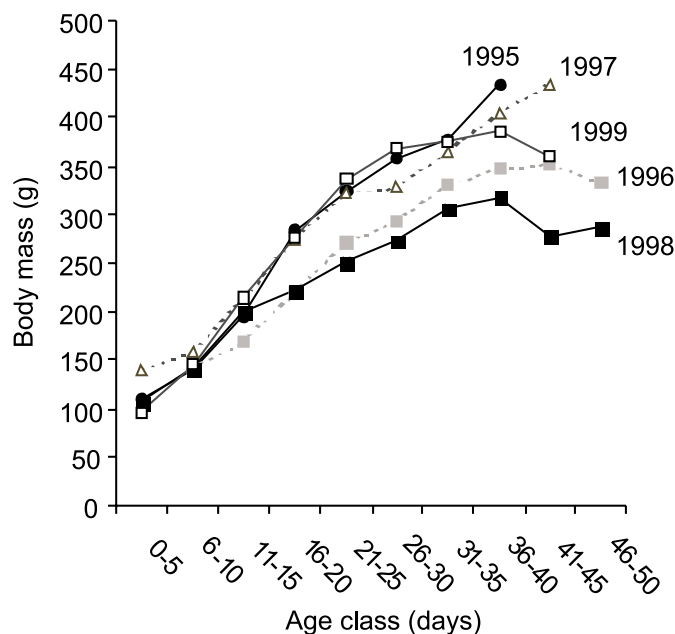
There was significant variation among years in the rate of chick mass increase (Table 3); mass increase was much slower in 1998 than in other years. This was due to a marked difference in the rate of mass increase at 15–30 days of age (Fig. 2; one-way ANOVA, $F_{[4,71]} = 7.3$, $P < 0.001$), whilst there was no difference in mass increase at 0–15 days of age (Fig. 2; one-way ANOVA, $F_{[4,51]} = 1.2$, $P = 0.337$). In addition to the rate of mass increase, chick body mass at age 30 ± 3 days also varied significantly among years (Table 4; one-way ANOVA, $F_{[3,53]} = 10.2$, $P < 0.001$), with chicks in 1999 heavier than chicks in 1996 and 1998.

There was significant variation among years in wing-growth rates of chicks (Table 3), which were highest in 1997 and lowest in 1998. Wing lengths of chicks aged 30 ± 3 days varied among years (one-way ANOVA, $F_{[3,53]} = 4.2$, $P = 0.01$), with wings significantly longer in 1999 than in 1998 (Table 4). Culmen and tarsus growth rates did not vary significantly among years (Kruskal–Wallis ANOVA for non-normal data; Table 3). Chick tarsus length at 30 ± 3 days of age was, however, less in 1998 than in 1997 or 1999 (Table 4; one-way ANOVA, $F_{[3,53]} = 9$, $P < 0.001$), but there

Table 3. Linear growth of Horned Puffin chicks at Duck Island in different years.

Year	Body mass (g/day)			Wing length (mm/day)			Culmen length (mm/day)			Tarsus length (mm/day)		
	Mean	n	SD	Mean	n	SD	Mean	n	SD	Mean	n	SD
1995	12.8 b	14	3.1	3.9 ab	14	1.05	0.39 a	14	0.08	0.37 a	15	0.08
1996	9.4 b	18	2.6	3.5 ab	18	0.91	0.28 a	11	0.16	0.39 a	12	0.21
1997	10.5 b	16	3.3	4.3 a	16	0.57	0.39 a	11	0.11	0.46 a	13	0.10
1998	3.7 a	22	6.9	3.4 b	22	1.08	0.27 a	10	0.13	0.30 a	12	0.16
1999	9.6 b	21	3.0	4.0 ab	21	0.43	0.29 a	10	0.13	0.36 a	10	0.10
Treatment	$F_{[4]} = 11.7, P < 0.001$			$F_{[4]} = 3.33, P = 0.014$			$H_{[4]} = 8.3, P = 0.081$			$H_{[4]} = 6.51, P = 0.164$		
Error	86			86								

Note: Means followed by different letters are significantly different as determined from Tukey's multiple-comparison tests.

Fig. 2. Increase in body mass of Horned Puffin chicks in different years.

was no significant variation in culmen length at age 30 ± 3 days of age among years (Table 4; $F_{[3,51]} = 2.35, P = 0.1$).

Chick fledging ages were recorded in 1996 (42 ± 4.9 days (mean \pm SD); $n = 25$), 1998 (35 ± 5.7 days; $n = 23$), and 1999 (41 ± 4.1 days; $n = 28$). The overall range of fledging ages among all 3 years was 29–49 days. There was significant variation among years (one-way ANOVA, $F_{[2,69]} = 15.66, P < 0.001$), with chicks fledging at the youngest ages in 1998.

Chick diet

A total of 1738 prey items were collected between 1995 and 1999. Sand lance (*Ammodytes hexapertus*) was the dominant prey species numerically, constituting $\geq 90\%$ of the chick diet in each year (Table 5). The other principal prey were capelin (*Mallotus villosus*) and salmon (*Oncorhynchus* sp.). Invertebrates comprised $< 0.5\%$ of the chick diet, on average.

Sand lance varied significantly among years in length (Table 6; one-way ANOVA, $F_{[4,1029]} = 9.2, P < 0.001$), mass ($F_{[4,985]} = 13.6, P < 0.001$), and predicted energy content ($F_{[4,718]} = 5, P < 0.001$).

Bill-load mass over all 5 years was 16.4 ± 6.4 g (mean \pm SD; $n = 64$), and the number of prey items per load was 6.2 ± 3.4 (mean \pm SD; $n = 131$). There was no significant variation among years in either the mean mass of prey per load (Table 7; one-way ANOVA, $F_{[3,57]} = 0.8, P = 0.97$) or the mean number of prey items per load ($F_{[3,124]} = 1.54, P = 0.2$).

Discussion

This study was spatially and temporally coincident with the major ENSO event of 1997–1998 that drove changes in water temperature and salinity, mixed water layer depth, nutrient upwelling, and phytoplankton production across the

Table 4. Body mass and external measurements of Horned Puffin chicks at 30 ± 3 days in age in different years.

Year	Mass (g)			Wing length (mm)			Tarsus length (mm)			Culmen length (mm)		
	Mean	n	SD	Mean	n	SD	Mean	n	SD	Mean	n	SD
1996	325.0 a	14	45.8	123.4	14	12.1	29.7	14	1.3	28.5	13	1.6
1997	337.9	10	51.6	128.3	10	10.8	30.4 a	10	1.3	28.5	10	2.0
1998	285.8 b	16	43.6	119.2 a	16	8.2	28.6 ab	16	1.3	28.4	16	1.9
1999	375.0 ab	17	48.2	131.0 a	17	10.4	30.7 b	17	1.3	29.8	16	1.6

Note: Means followed by different letters are significantly different as determined from Tukey's multiple-comparison tests.

Table 5. Composition of the Horned Puffin chick diet at Duck Island.

Prey item	1995		1996		1997		1998		1999	
	n	%	n	%	n	%	n	%	n	%
Pacific sand lance (<i>Ammodytes hexapterus</i>)	91	98	825	94	465	95	158	90	103	99
Capelin (<i>Mallotus villosus</i>)	2	2	27	3	9	2	3	2	0	0
Salmon (<i>Oncorhynchus</i> sp.)	0	0	16	2	7	1	8	5	1	1
Pacific lamprey (<i>Lampetra tridentatus</i>)	0	0	4	1	0	0	2	1	0	0
Cod sp. (Gadidae)	0	0	0	0	2	0	0	0	0	0
Euphasiid	0	0	0	0	6	1	1	<1	0	0
Sculpin sp. (Cottidae)	0	0	0	0	1	0	0	0	0	0
Sandfish (<i>Trichodon trichodon</i>)	0	0	1	0	0	0	0	0	0	0
Unidentified smelt (Osmeridae)	0	0	0	0	0	0	1	<1	0	0
Unidentified fish species	0	0	0	0	0	1	2	1	0	0
Total prey items	93		873		490		175		104	

Table 6. Mean size and energy content of sand lance in Horned Puffin chick diets in different years.

Year	Body length (mm)				Mass (g)				Energy content (kJ)		
	Mean	n	SD	Range	Mean	n	SD	Range	Mean	n	SD
1995	92.7 abc	93	24.7	45–180	2.9 bcd	93	2.6	0.5–21.0	16.1 ab	93	15.2
1996	85.2 a	542	31.5	47–223	2.1 a	560	1.8	0.3–14.3	13.8 b	293	10.1
1997	86.0 ac	143	19.1	57–164	2.5 ad	142	2.3	0.6–18.7	13.1 b	142	13.7
1998	93.0 bc	158	16.2	51–146	2.7 bcd	94	1.5	0.5–7.8	14.4 ab	94	8.0
1999	100.2 b	101	8.5	64–123	3.3 bc	104	1.0	0.8–7.0	18.7 a	101	6.2

Note: Means followed by different letters are significantly different as determined from Tukey's multiple-comparison tests.

Table 7. Horned Puffin bill loads (complete chick meals).

Year	Mass per load (g)				No. of prey items per load			
	Mean	n	SD	Range	Mean	n	SD	Range
1995	15.2	3	4.2	12.0–20.0	7.7	3	3.8	5–12
1996	17.4	15	8.1	2.5–34.5	6.9	16	2.8	4–15
1997	16.0	16	7.2	6.6–32.0	6.3	67	3.3	1–22
1998	16.5	8	7.1	7.8–21.5	6.0	24	3.4	1–13
1999	15.7	22	6.1	6.4–25.6	4.9	21	1.8	2–8
1995–1999	16.4	64	6.4	2.5–34.5	6.2	131	3.4	1–22

North Pacific Ocean (Goes et al. 2001; Whitney and Welch 2002). Negative effects of ENSO-related anomalous oceanographic and biological conditions on seabird species in the North Pacific Ocean included delayed breeding (Bertram et al. 2001), reduced reproductive success (Gaston and Smith 2001), and a major mass-mortality event (Baduini et al. 2001).

On the local scale, oceanographic data from Cook Inlet indicate that the 1997–1998 ENSO event resulted in reduced salinity of surface water in the vicinity of Duck Island and an increase of 1–2°C in winter water temperature (Piatt et al. 1999; Piatt 2002). In association with these locally anoma-

lous oceanographic conditions, the catch per unit effort of fish (principally sand lance) in beach seines (Piatt 2002) was lower (mean = 23 fish/set; $n = 21$ sets) in 1998 than in other years (1995–1997, 1999) of study (mean range = 31–64 fish/set; $n = 94$ sets).

Two lines of indirect evidence also suggest that prey were relatively unavailable to seabirds in Cook Inlet in 1998: (1) large numbers of Common Murres (*Uria aalge*) died en masse throughout Cook Inlet in 1998 (Piatt et al. 1999) and (2) murres on Duck Island exhibited almost complete breeding failure in 1998 (Piatt et al. 1999), in contrast to high

breeding success in the other 4 years of this study. The diet of murres on Duck Island considerably overlaps that of the Horned Puffins, comprising 24% sand lance, on average (Piatt 2002). Murres have the ability to switch prey, and normally have considerable flexibility in their time and activity budgets, allowing them to increase their foraging effort in response to a reduction in food supply (Monaghan et al. 1994; Uttley et al. 1994; Zador and Piatt 1999). We therefore assume that their breeding failure indicates that forage-fish availability to seabirds was exceptionally poor in the waters around Duck Island in 1998, in association with the ENSO event of 1997–1998.

Annual variation and the effects of El Niño on Horned Puffins

Productivity

Breeding failure has rarely been recorded in the Horned Puffin, and variability in the reproductive success of Horned Puffins among years and colonies is quite low (Piatt and Kitaysky 2002). We also found no significant variation among years in Horned Puffin breeding success at Duck Island. These results should be viewed with caution, however, since only a small proportion of chicks (ca. 50%) were followed to fledging each year. Moreover, the data from this and most other studies are limited by a lack of knowledge of the proportion of birds that attempt to breed, and do not include a measure of incubation success, which may be a key factor for overall reproductive success in puffins (Hatch and Hatch 1990). Complete breeding failure resulting from poor food availability has been reported in the Atlantic Puffin, but has been always linked to an extreme food shortage associated with overfishing (e.g., Lid 1981; Anker-Nilssen 1987; Barrett et al. 1987; Martin 1989; Barrett and Rikardsen 1992).

Chick growth and fledging

The rates of mass increase of Horned Puffin chicks at Duck Island were exceptionally low in 1998, presumably reflecting poor food availability in the surrounding waters. Food limitation is known to reduce the daily growth rates of Atlantic Puffin chicks (Harris 1984), and is well documented from both experimental (Harris 1978; Hudson 1979; Øyan and Anker-Nilssen 1996) and field studies (e.g., Tschanz 1979; Harris 1985; Barrett et al. 1987; Barrett and Rikardsen 1992).

The impacts of a reduced food supply on growth varied among body structures, suggesting differential allocation of energy and nutrients. Differences in chick size at 30 ± 3 days of age were most pronounced for body mass and wing length, with a smaller difference in tarsus length and no difference in culmen length. These results are similar to the results of experimental studies of Atlantic Puffins (Øyan and Anker-Nilssen 1996), Horned Puffins, and Tufted Puffins (*Fratercula cirrhata*; Kitaysky 1996), which showed that under conditions of reduced food supply, highest priority was given to the growth of the skull and bill and lowest priority to that of the tarsus. Wing feathers can continue to grow after fledging, and slightly shorter wings at fledging will not necessarily reduce flight or diving performance, since body mass at fledging is also lower under conditions of poor food supply.

The increase in chick mass in 1998 was sharply reduced after chicks reached about 15 days of age. Atlantic Puffin chicks receive most food in the middle third of their 6-week development (Harris 1984), when the combined requirements of body maintenance and growth are highest. Because of low food availability, Horned Puffin parents on Duck Island in 1998 may have been unable to increase their provisioning rates as chick requirements increased with age. The reduction in growth after chicks reached 15 days of age may also reflect a decrease in local food availability during the second half of chick rearing.

The total range of fledging ages in this study was 29–49 days, slightly wider than ranges previously recorded in the field (Amaral 1977; Wehle 1980; Petersen 1983), although earlier data were based on very small sample sizes. Nest-site departures were unusually early in 1998. This could be ascribed to relatively high prefledging mortality, with starving chicks departing the nest site prematurely. However, several lines of evidence suggest that chicks simply fledged at an earlier age: (i) In contrast to studies on Atlantic Puffin colonies during seasons of breeding failure and nestling starvation (e.g., Lid 1981), no chicks were observed either depredated or dead outside nest sites or near their nest entrance in this study; (ii) feather development in the youngest fledglings in 1998 was similar to that in chicks fledging in other years, with very little or no down present; (iii) although the youngest fledglings in 1998 may have been unable to fly from the nest, flight is not a requirement for Horned Puffins to fledge. Whereas Atlantic Puffin fledglings fly from the colony (Harris 1984), Horned Puffin chicks may fledge by flying or by walking from the nest site directly to the water (Piatt and Kitaysky 2002). Nest sites on Duck Island are within 20 m of the shore and in other years puffin fledglings have been observed to walk to the water's edge before swimming away from the colony (A.M.A. Harding, personal observation); (iv) evidence for a positive relationship between body mass at fledging and postfledging survival has not been found in Atlantic Puffins (Harris 1984; Harris and Rothery 1985), and Ydenberg (1989) suggests that since puffins fledge at only approximately 70% of adult body mass, fledgling size may not be as closely linked to postfledging survival in puffins as it is in species that complete their growth at the nest site. Thus, although we cannot be certain of successful fledging of young chicks in 1998, we assume that chicks fledged at a younger age rather than that prefledging mortality was high.

The wide range of fledging ages observed on Duck Island indicates that Horned Puffins have a high degree of flexibility in fledging age. Flexibility in fledging age is usually interpreted as a trait associated with highly variable and unpredictable food supplies (Lack 1968), and the wide range of puffin growth rates and fledging ages recorded in the wild (e.g., Nettleship 1972; Harris 1984) probably reflects a range of feeding conditions. The fledging ages of Horned Puffins in 1998 contrast with the older fledging ages of the Atlantic Puffin in conditions of poor food supply (e.g., Nettleship 1972; Anker-Nilssen 1987; Barrett et al. 1987; Barrett and Rikardsen 1992; Ydenberg et al. 1995). The assumed younger fledging ages in 1998 may have resulted from adults abandoning breeding to preserve their future reproductive potential. Alternatively, chicks may have fledged early as an adaptive response to low food availability, if they could

achieve higher growth rates by foraging for themselves at sea than by depending on their parents delivering food from distant foraging areas.

Chick diet

Annual or seasonal change in chick diet associated with a reduction in local food availability has been well documented (e.g., Lid 1981; Hislop and Harris 1983; Martin 1989; Baird 1990; Barrett and Furness 1990). For example, increased diversity in the diet of Atlantic Puffin chicks has been recorded during seasons of poor food availability (Barrett et al. 1987; Barrett and Rikardsen 1992), with breeding failure observed in colonies without access to alternative prey (Martin 1989; Barrett and Rickardsen 1992).

Although the sand lance is a dominant prey species for Horned Puffin chicks, changes in chick diet composition have been observed in response to large-scale shifts in forage fish species composition in the Gulf of Alaska (Piatt and Kitaysky 2002). These documented changes in chick diet and the higher diversity of prey items observed in the adult's winter diet, including myctophids and squid (Piatt and Kitaysky 2002), suggest that although the chick diet is highly dependent on sand lance, Horned Puffins do have the ability to feed on a variety of species and switch prey if there is a change in composition or abundance of the prey base.

However, there was no change in chick diet composition over the 5 years of this study, even during 1998, the year of suspected food shortage. Sand lance remained the dominant prey species, comprising $\geq 90\%$ of the chick diet in all years. Relative prey abundance is important in determining chick diet composition when food availability is reduced. Data from annual midwater trawl surveys conducted in Lower Cook Inlet suggested that although the absolute abundance of sand lance was lower in 1998, relative abundance was high compared with that of other species of forage fish (Piatt 2002). This suggests that although food resources were generally low in 1998, sand lance dominated the local forage fish species, allowing Horned Puffins to continue to specialize on sand lance as food for chicks.

In the Atlantic Puffin, the frequency of chick feeds (Martin 1989; Barrett and Rickardsen 1992) and the mass of bill loads (Harris 1985; Barrett et al. 1987; Martin 1989; Nettleship 1991; Barrett and Rikardsen 1992) have been commonly observed to decrease in years of poor food availability. There is also evidence of reduced rates of meal delivery to Tufted Puffin chicks during the food shortages associated with the El Niño event of 1991–1993 (Bailey et al. 1995). In this study there was no observed variation among years in bill-load mass or derived/predicted energy content. Horned Puffins at Duck Island forage at long distances from the colony: at-sea surveys in Lower Cook Inlet recorded Horned Puffins regularly foraging 50–110 km from Duck Island (Piatt and Kitaysky 2002). In accordance with the economic foraging perspective of central place foraging theory (Schoener 1979; Kacelnik and Cuthill 1990), Horned Puffins foraging at long distances from Duck Island should always maximize their bill-load mass per journey, so low food availability would be expected to affect the frequency of feeding chicks rather than meal size.

Summary

This study has provided a more detailed understanding of the breeding ecology of Horned Puffins than was previously available, particularly by extending our knowledge of chick development patterns, adult food loads, and annual variability in breeding parameters. Horned Puffins were able to maintain high fledging success over the 5 years of this study despite poor local feeding conditions and the almost complete breeding failure of Common Guillemots (*Uria aalge*) at the same colony in 1998. The ability of Horned Puffins to successfully rear a chick over a wide range of food availability reflects a number of adaptations for exploiting a variable and sometimes scarce food supply. These adaptations include flexibility in chick development and fledging age, and differential allocation of limited food resources to different body structures. Puffins are also able to adjust the number of fish carried per chick meal delivery, unlike the Common Guillemot, which carries only one prey item at a time. In addition to these physiological and behavioural adaptations, burrows may provide puffins with an ecological buffer that affords protection against adverse weather and avian predators during chick rearing, allowing parents the added flexibility to forage simultaneously and (or) increase foraging-trip duration. The results of this study suggest that chick growth rates, particularly in body mass, may be sensitive indicators of local food availability, and may be a good parameter for use in monitoring Horned Puffins.

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